Science of the Total Environment 659 (2019) 756–763

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Life history responses of spring-and autumn-germinated ephemeral plants to increased nitrogen and precipitation in the Gurbantunggut Desert

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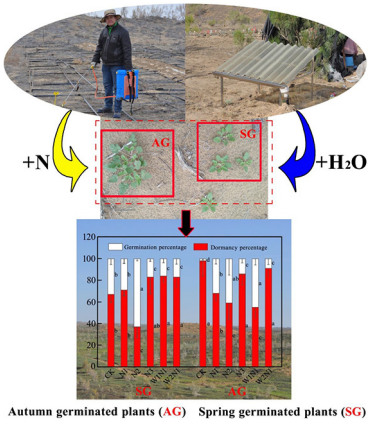
HIGHLIGHTS

- Increased nitrogen and precipitation plus nitrogen treatments significantly improved survival of spring- and autumn-germinated plants.
- Increased nitrogen inhibited growth of spring- and autumn-germinated plants, but precipitation plus nitrogen have an improvement.
- Spring- and autumn-germinated plants produced seeds of different dormancy levels.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 14 November 2018
Received in revised form 24 December 2018
Accepted 24 December 2018
Available online 31 December 2018

Editor: Elena PAOLETTI

Keywords:
Cold desert
Ephemeral plant
Erodium oxyrhynchum

ABSTRACT

Nitrogen deposition and precipitation change are not only hot topics of current global change but also the main environmental factors affecting plant growth. Thus, the effects of nitrogen and precipitation on the life history of spring- (SG) and autumn-germinated (AG) ephemeral plants of *Erodium oxyrhynchum* were researched in the Gurbantunggut Desert, northern China, and the aim was to understand the response of plants from different germination seasons to global change. SG and AG plants with increased nitrogen and precipitation plus nitrogen treatments were measured to determine seedling survival, phenology, plant traits, biomass accumulation and allocation and dormancy characteristics of offspring (seeds). The results showed that increased nitrogen and precipitation plus nitrogen treatments significantly improved the survival of SG and AG plants during the seedling stage, and precipitation plus nitrogen treatments also improved the growth and seed production of SG and AG plants, but increased nitrogen significantly inhibited their growth and seed production. Therefore, precipitation plays an important role in regulating nitrogen uptake by plants in arid and semiarid ecosystems. With increased nitrogen, SG and

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https://doi.org/10.1016/j.scitotenv.2018.12.368
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Increased nitrogen
Increased precipitation
Climate change

AG plants allocated more biomass into root and reproductive organs but allocated significantly less biomass into the leaf, with almost no change in biomass allocation to the stem. With nitrogen plus precipitation treatments, biomass allocation in all organs of SG and AG plants showed almost no change. Clearly, changes in soil moisture also affected biomass allocation of SG and AG plants. For offspring dormancy, SG and AG plants produced more nondormancy seeds with increased nitrogen but produced more dormancy seeds under precipitation plus nitrogen treatments. Hence, in a harsh environment, SG and AG plants produced more nondormancy offspring with low reproduction in order to occupy the habitat rapidly in the following year or produced more dormancy offspring with high reproduction in a suitable environment intended for spreading germination risk in time and conserve the population.
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1. Introduction

Nitrogen has been identified as one of the constraining factor of plant growth for a long time, ever since Liebig's 'law of the minimum', which led to research that crop yield is limited by the nutrient in shortest supply (Thomas, 1929). Therefore, nitrogen fertilization is widely used to improve plant growth (Frink et al., 1999), which leads to nitrogen deposition that has increased by three to five fold over the past century (Solomon et al., 2007; Gruber and Galloway, 2008; Boutin et al., 2017). Plants as the primary producers in terrestrial ecosystems are inevitably affected by nitrogen deposition (Walters and Reich, 2000; Villar-Salvador et al., 2012), but the effects of nitrogen deposition on plants mainly focus on community-level indicators, such as diversity (LeBauer and Treseder, 2008; Ochoa-Hueso et al., 2011), vegetation coverage (McHugh et al., 2017), community biomass (Xu et al., 2018) and plant-plant interactions (Wang et al., 2016). Studies on the effects of nitrogen deposition at the species level only involve the flowering and fruiting date (Whitford and Gutierrez, 1989), biomass accumulation (Wang et al., 2016), and yield (Yan et al., 2017). Therefore, studies on the effects of nitrogen on plant life history are especially lacking.

Water is an important component of protoplasts and affects nitrogen transport in plants (Siefritz et al., 2004; Navarro et al., 2003). Due to climate warming, precipitation pattern is changing from regional to global scale (Stocker et al., 2013) and is also affecting nitrogen uptake and utilization of plants. Previous research shows that the interaction of nitrogen and precipitation significantly advances plant phenology (Huang et al., 2018), improves root growth (Zhang et al., 2017), increases leaf number (Huang et al., 2018) and biomass accumulation (Al-Solaimani et al., 2017), and increases yield (Altenbach et al., 2003; Fuertes-Mendizabal et al., 2010). Thus, when soil moisture is sufficient, the effects of nitrogen on plant growth are more significant than those of only an increase in nitrogen.

In arid and semiarid regions, water and nitrogen (N) are the most important limiting factors for plant growth (Ehleringer et al., 1998; Allah et al., 2014). In the past 30 years, nitrogen deposition increased by 3 kg N ha^{-1} (Liu et al., 2013; Xu et al., 2015) and annual precipitation increased by 24.4 mm in northwest China (Shi, 2003; Bai et al., 2008; Liu et al., 2010), and these increasing trends will be maintained in this century (Huang et al., 2017). In the Gurbantunggut Desert of northwest China, plants include winter annuals and/or spring ephemerals, summer annuals, and herbaceous perennials or woody perennials (Huang et al., 2018). Winter annuals and/or spring ephemerals have fast growth rates and high light-use efficiency, and a high proportion of their biomass is allocated to reproduction (Yuan and Tang, 2010). Thus, winter annual and/or spring ephemeral plants are extremely sensitive to current global change.

Previous research found that some ephemeral species have two germination seasons: spring and autumn. When rainfall is abundant in autumn, the seeds of ephemeral plants can germinate in autumn, overwinter in the form of seedlings, and complete the life cycle in the spring of the following year (Lu et al., 2012; Lu et al., 2014; Lu et al., 2016). When rainfall is scarce in autumn, seed germination is delayed until the following spring, and plants quickly complete their life cycle in spring and early summer (Lu et al., 2012), such as *Planta gominuta* (Zhang et al., 2007), *Astragalus arpilobus* (Long et al., 2012), *Isatis violascens* (Zhou et al., 2015) and *Diptychocarpus strictus* (Lu et al., 2014). Due to the different germination seasons, most life history traits of spring- and autumn-germinating plants are obviously different, including post-germination lifespan (Lu et al., 2014; Lu et al., 2016), plant size (Wang et al., 2010), fruit production (Zhang et al., 2007), biomass accumulation (Lu et al., 2014; Lu et al., 2016;) and dormancy of offspring (seeds) (Wang et al., 2010). Therefore, research on the response of spring- and autumn-germinating plants to increased nitrogen and precipitation is extremely important to predict the future development of the population.

Erodium oxyrhynchum (Geraniaceae) is the most common spring- and autumn-germinating ephemeral plant in the Gurbantunggut Desert (Huang et al., 2016; Jia et al., 2018). The species occurs in Kazakhstan, the Caucasus, western Asia and China and is widely distributed in the Gurbantunggut Desert (Xu and Huang, 1998). In May, the coverage rate of *E. oxyrhynchum* reaches 40%, while the coverage rate of the long-lived herbs and shrubs is <10% in this area (Wang et al., 2003). *E. oxyrhynchum* is the main contributor to stabilize sand dunes in the Gurbantunggut Desert in early spring (Wang et al., 2003). Research shows that autumn-germinated plants are significantly larger and produce more seeds than spring-germinated plants (Wang et al., 2006; Zhang et al., 2007). Based on significant differences in plant traits between spring- and autumn-germinating plants, we proposed the hypothesis that the life history of spring-and autumn-germinating plants would differ in the response to an increase in nitrogen and precipitation plus nitrogen treatments in the field. To test the hypothesis, we compared the phenology, survival, plant traits, biomass accumulation and allocation and offspring (seeds) germination of spring- and autumn-germinated plants with increased nitrogen and precipitation.

2. Materials and methods

2.1. Study site

The study area is at the southern margin of the Gurbantunggut Desert. The range of the Gurbantunggut Desert is from 44°11′ to 46°20′ N and 84°31′ to 90°00′ E, and the desert covers an area of approximately 4.88×10^4 km^2 as the largest fixed and semifixed desert in China (Wang et al., 2004). The Gurbantunggut Desert has a typical temperate continental climate with hot summers and cold winters, and mean annual precipitation is 70–180 mm (Fan et al., 2014). Especially, a continuous snow cover occurs in winter, and snow melting provides sufficient moisture for the growth of ephemeral plants in early spring (Zhou et al., 2009), such as *E. oxyrhynchum*, *Alyssum linifolium*, *Malcolmia scorpioides*, *Schismus arabicus*, *Nepeta micrantha*, and *Eremopyrum distans*, among others (Wang et al., 2003).

2.2. Experimental design

2.2.1. Increased nitrogen and precipitation-nitrogen interaction experiments

The amount of nitrogen deposition in Urumqi City (the nearest city from the study area) has reached 35.4 kg ha^{-1} yr^{-1} (Wei, 2015). Considering the trend of nitrogen deposition in the future (Galloway et al.,

2008), we simulated four nitrogen deposition levels in the experiment: CK (control treatment, no additional nitrogen input, the value was equal to the actual nitrogen input), N1 (equated to the current deposition rate in Urumqi City of approximately 30 kg N ha^{-1} yr^{-1}), N2 (simulated the trend of nitrogen deposition in the future of approximately 60 kg N ha^{-1} yr^{-1}), and N3 (simulated the extreme nitrogen deposition of approximately 120 kg N ha^{-1} yr^{-1}). Precipitation is predicted to increase by 30% in northern China in the next 30 years, and precipitation fluctuations may reach +50% in extreme precipitation years (Liu et al., 2010). Therefore, we set up +30% and +50% increases in precipitation to simulate future and extreme precipitation amounts, respectively, which interacted with the N1 treatment. Therefore, the field experiment included six treatments (CK, N1, N2, N3, W1N1 and W2N1) with four replicates for observations of phenology and four replicates for biomass sampling. We implemented a randomized experimental design at the bottom of dunes.

To avoid interspecific competition, we weeded out other plants in the plots between November 2016 and April 2017. At the same time, all plots were surrounded by plastic film to prevent interference from the outside. To collect natural precipitation (rainfall and some snow) in spring and summer for use in the precipitation plus nitrogen treatments, we also set up four rainfall collectors. Each rainfall collector consisted of a plastic board (4 m × 4 m, area of 16 m^2) set at an angle of 30° to the ground, the four corners of the board fixed to an iron pole, and a bucket placed at the lower corner of the board to collect rainfall.

To monitor precipitation, temperature, and soil moisture of the study area, a weather and soil moisture monitoring device (Caipos GmbH, Schiller Strasse Gleisdorf, Austria) was installed in the study area on September 2016, and the device collected environmental data via wireless sensors and uploaded them to an indoor computer every hour. According to the precipitation data, we increased precipitation to the plots (including some snow) using a watering can to water plants. The total precipitation amount in a life history cycle was 48 mm (only events with >5 mm of precipitation were considered), and 12.5 and 24.0 L of water were added to the plots of W1N1 and W2N1, respectively. According to the Zhou et al. (2011) method of nitrogen application, nitrogen was applied twice a year in late March (melting of snow) and late October (before snowfall). When nitrogen was applied, NH_4NO_3 and NH_4Cl were dissolved in water by NH_4: NO_3 at 2: 1 and manually sprayed evenly on the surface of plots; the same amount of water was sprayed on the controls. Finally, we built a 50 m × 50 m fence to prevent interference from wildlife and human activities.

2.3. Experimental material

The density of *E. oxyrhynchum* plants in the field reaches 96.5 plants/m^2 (Chen et al., 2008); thus, the number of plants was enough for the experiments. On October 10, 2016, 12 AG plants were marked using a red wire in each plot, and on March 10, 2017, we marked the SG plants with the same method (Supplementary Fig. 1).

2.4. Measurement and sampling

2.4.1. Phenology

12 plants were randomly selected for phenological observations in each treatment. We referred to the Lu et al. (2014) method of phenological observations and checked the experimental plots every 3 days from seed germination to plant death. The emergence date, flowering date, fruiting date and maturation date were recorded. Then, the lifespan of plants (emergence of the first individual until the death of the last individual) was determined.

2.4.2. Survivorship

From germination to death, we recorded the number of surviving plants every 3 days in all treatments.

2.4.3. Morphological characters

When the plants reached maturity, plant traits of 12 plants in each treatment (plant height, leaf area, root length, number of branches, leaves, and seeds) were measured. For leaf area, we collected all leaves and measured them using a LI-COR 3000 leaf area meter (Li-Cor Inc., Lincoln, NE, USA). Root length was measured from the root collar to the tip of the main root. For branch number, we counted all branches on the main stem.

2.4.4. Dry mass accumulation and allocation

When the fruit began to turn yellow-orange, we harvested seeds from plants. Because seed maturity did not occur at the same time among different treatments, we harvested seeds and plants on different dates. After plant traits were measured, plants were separated into roots, stem, leaves and reproductive organs (including flowers, fruits, seeds), and roots were carefully washed free of soil. Then, roots, stems, leaves and reproductive organs were dried at 75 °C for 48 h and weighed using a Sartorius BS210S electronic-balance (0.0001 g). Total biomass was calculated as the sum of roots, stems, leaves and reproductive organs. Biomass allocation to roots, stems, leaves and reproductive organs was expressed as a percentage as follows:

$$\text{Root allocation} = (\text{roots mass})/(\text{total mass}) \times 100\%;$$

$$\text{Stem allocation} = (\text{stems mass})/(\text{total mass}) \times 100\%;$$

$$\text{Leaf allocation} = (\text{leaves mass})/(\text{total mass}) \times 100\%;$$

$$\text{Reproductive allocation} = (\text{reproductive mass})/(\text{total mass}) \times 100\%.$$

2.4.5. Offspring (seed) germination

Mature fruits of AG and SG plants from different treatments were collected from May 21 to June 1, 2017, and the long awn of fruits was removed for germination tests. Germination tests were conducted at an alternating temperature regime of25/10 °C (12/12 h) (unpublished), starting on June 20, 2017. Twenty-five seeds were placed in each Petri dish (7-cmdiameter petri dishes) on two layers of Whatman No. 1 filter paper moistened with 3 mL of distilled water. Water was added to keep the filter paper moist during the test period. Seeds were considered germinated when the radicle emerged and were removed every day for 30 days. The final percentage of germination (FPG) was estimated as follows: FPG = GN/SN, where GN is the total number of germinated seeds and SN is the number of viable seeds. After the germination trials were completed, the nongerminated seeds were tested for viability using the TTC method (Baskin and Baskin, 2014).

2.5. Statistical analyses

Data were arcsine (percentage data) or log10 (other data) transformed before conducting factor analyses to approximate the normal distribution and homogeneity of variance to fulfill the assumptions of two-way ANOVA. If the variance of transformed data was still not homogenous, treatment differences in these characteristics were assessed using the Kruskal-Wallis test. Then, all life traits were analyzed as dependent variables with a two-way ANOVA, germination seasons and environment factors (nitrogen and precipitation) were considered fixed effects, and all treatments terms were included. To survivorship, multivariate survival analyses were carried out by the methods of Kaplan-Meier. Tukey's HSD test was performed for multiple comparisons to determine significant differences among treatments, and results were considered significant when $p < 0.05$. Pearson correlations were initially calculated for data from the experiment, including for plant traits and dry mass accumulation and allocation. All data analyses were performed with the SPSS 13.0 statistical software package (SPSS

Inc., Chicago, Illinois, USA). All figures were drawn with Origin software 2015 (Origin Lab, Northampton, MA).

3. Results

3.1. Phenology

The AG plants germinated (CK) on October10, 2016, but SG plants germinated (CK) on March 30, 2017, and the main phenophases (seedling emergence date, flowering date, fruiting date, yellowing date and life cycle) of AG plants were significantly earlier than those of SG plants ($p < 0.05$). Increased nitrogen (N1, N2, N3) had no significant effect on the main phenophases of SG and AG plants (Table 1), but precipitation plus nitrogen treatments (W1NI and W2N1) delayed the main phenophases of SG and AG plants significantly ($p < 0.05$, Table 1).

3.2. Survivorship

Results of Kaplan–Meier Survival Analysis showed that survival of AG and SG plants (CK) declined sharply in early April 2017, and survival of AG plants (64.5%) was significantly lower than that of SG plants (81.3%) ($p < 0.05$, Fig. 1a–b). Increased nitrogen (N1, N2, N3) improved the survival of SG and AG plants significantly ($p < 0.05$): survival of SG plants increased from 81.3% (CK) to 85.8% (N1), 100.0% (N2) and 97.7% (N3), and survival of AG plants increased from 64.5% (CK) to 74.7% (N1), 83.5% (N2), and 97.8% (N3) (Fig. 1a–b). Similarly, precipitation plus nitrogen treatments (W1NI and W2N1) also improved the survival of SG and AG plants significantly ($p < 0.05$): survival of SG plants increased from 81.3% (CK) to 91.7% (W1N1) and 86.2% (W2N1), and survival of AG plants increased from 64.5% (CK) to 83.6% (W1N1) and 81.3% (W2N1) (Fig. 1a–b).

3.3. Plant traits

In the control (CK), most life history traits of AG plants (height, leaf area, root length, leaf number and seed number) were significantly greater than those of SG plants ($p < 0.05$, Table 2), except for branch number ($p = 0.89$, Table 2). Height and branch number of SG plants showed almost no change with increased nitrogen (N1, N2, N3), but increased nitrogen (N1, N2, N3) led to decreased leaf area, leaf number, branch number and seed number and shortened root length of SG plants. With increased nitrogen (N1, N2, N3), leaf area, root length, leaf number and seed number of AG plants also showed a decreasing trend, but height and branch number of AG plants showed no response to increased nitrogen (Fig. 2a–f). Precipitation plus nitrogen treatments (W1NI and W2N1) increased the height, leaf area and seed number of SG plants significantly but had no significant impact on other traits (root length, leaf number and branch number) of SG plants. Precipitation plus nitrogen treatments increased the leaf area and leaf number of AG plants and also shortened the root length of AG plants ($p < 0.05$, Fig. 2a–f); other traits (height, branch number and seed number) of AG plants were not significantly affected.

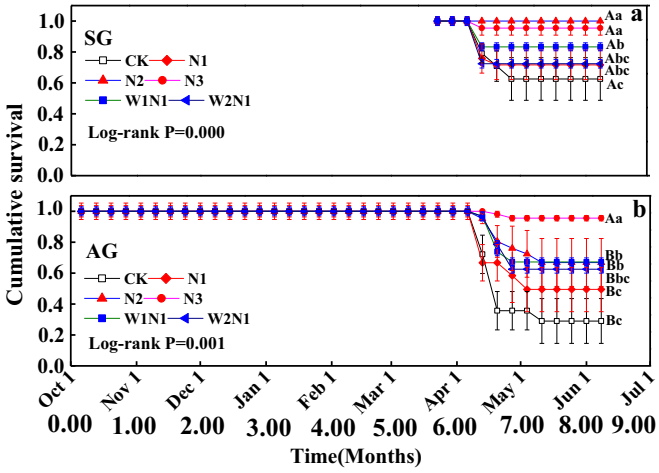

Fig. 1. Kaplan–Meier Survival Curve of spring- and autumn-germinated plants of *Erodium oxyrhynchum* in the treatments of increased nitrogen and precipitation plus nitrogen treatments. Note: Spring-germinated plants, SG; autumn-germinated plants, AG; control treatment, CK; 30 kg N ha^{-1} yr^{-1}, N1; 60 kg N ha^{-1} yr^{-1}, N2; 120 kg N ha^{-1} yr^{-1}, N3; +30% increases in precipitation plus 30 kg N ha^{-1} yr^{-1}, W1N1; +50% increases in precipitation plus 30 kg N ha^{-1} yr^{-1}, W2N1. Values represent means ± SE. Significant difference was observed among all treatments, different lowercase letters indicate significant differences among increased nitrogen and precipitation plus nitrogen treatments (CK, N1, N2, N3, W1N1 and W2N1) for SG and AG (Tukey HSD test, N = 4, $p < 0.05$), and different uppercase letters indicate significant differences between SG and AG at the same increased nitrogen or precipitation plus nitrogen treatments (*t*-test, N = 4, $p < 0.05$).

3.4. Dry mass accumulation and allocation

In the control (CK), total dry biomass of AG plants was significantly heavier than that of SG plants ($p < 0.05$, Table 2), which reached 0.88 and 0.53 g $plant^{-1}$, respectively. Increased nitrogen (N1, N2, N3) inhibited biomass accumulation of SG and AG plants ($p < 0.05$, Table 2), with reductions from 0.53 g (CK) to 0.47 g (N1), 0.43 g (N2) and 0.22 g (N3) $plant^{-1}$ for SG plants, and in AG plants, from 0.88 g (CK) to 0.83 g (N1), 0.50 g (N2) and 0.44 g (N3) $plant^{-1}$ (Fig. 3). By contrast, precipitation plus nitrogen treatments (W1NI and W2N1)

Table 1
Effects of increased nitrogen and precipitation plus nitrogen treatments on phenology of SG and AG plants of *Erodium oxyrrhynchum*.

Phenology	Spring-germinating plants						Autumn-germinating plants					
	CK	N1	N2	N3	W1N1	W2N1	CK	N1	N2	N3	W1N1	W2N1
Emergence date	30 March	30 March	30 March	30 March	30 March	30 March	10 October	10 October	10 October	10 October	10 October	10 October
Four-leaf rosette date	3 May	3 May	3 May	2 May	4 May	4 May	20 April	21 April	21 April	19 April	22April	21 April
Flowering date	12 May	13 May	12 May	11May	13 May	13 May	9 May	9 May	10 May	9 May	12 May	12 May
Fruiting date	14 May	14 May	14 May	13 May	15 May	15 May	11 May	12 May	12 May	12 May	13 May	13 May
Withering date	24 May	25 May	25 May	24 May	26 May	25 May	21 May	22 May	22 May	22 May	24 May	24 May
Life cycle (d)	55.14 ± 0.26^{Bbc}	56.63 ± 0.42^{Bab}	55.5 ± 0.37^{Bc}	55.6 ± 0.40^{Bc}	57.4 ± 0.27^{Ba}	57.88 ± 0.30^{Bab}	225.43 ± 0.43^{Ac}	226.86 ± 0.34^{Ab}	226.63 ± 0.26^{Ab}	226.10 ± 0.22^{Ab}	228.22 ± 0.15^{Aa}	228.89 ± 0.20^{Aa}

Note: Spring-germinated plants, SG; autumn-germinated plants, AG; control treatment, CK; 30 kg N ha^{-1} yr^{-1}, N1; 60 kg N ha^{-1} yr^{-1}, N2; 120 kg N ha^{-1} yr^{-1}, N3; +30% increases in precipitation plus 30 kg N ha^{-1} yr^{-1}, W1N1; +50% increases in precipitation plus 30 kg N ha^{-1} yr^{-1}, W2N1. Values represent means ± SE. Significant difference was observed among all treatments, different lowercase letters indicate significant differences among increased nitrogen and precipitation plus nitrogen treatments (CK, N1, N2, N3, W1N1 and W2N1) for SG and AG (Tukey HSD test, N = 8, $p < 0.05$), and different uppercase letters indicate significant differences between SG and AG at the same increased nitrogen or precipitation plus nitrogen treatments (*t*-test, N = 8, $p < 0.05$).

Table 2
Summary of a two-way ANOVA showing the effects of different germination seasons and increased nitrogen and precipitation treatments.

Plant traits	Source of variation	df	F	Sig.	Plant traits	F	Sig.
Height	S	1	31.578	<0.05	Leaf mass	18.382	<0.05
	NP	5	1.898	0.107		49.986	<0.05
	S × NP	5	0.904	0.484		1.948	0.099
Leaf area	S	1	30.426	<0.05	Reproduction	34.292	<0.05
	NP	5	15.008	<0.05	mass	7.407	<0.05
	S × NP	5	1.673	0.154		0.678	0.642
Root	S	1	4.663	<0.05	Total mass	20.52	<0.05
length	NP	5	15.059	<0.05		27.402	<0.05
	S × NP	5	2.397	<0.05		0.557	0.732
Leaf	S	1	20.347	<0.05	Allocation to root	2.112	0.151
number	NP	5	20.059	<0.05		7.798	<0.05
	S × NP	5	1.197	0.321		1.21	0.315
Branch	S	1	0.019	0.89	Allocation to	1.278	0.263
number	NP	5	2.629	<0.05	stem	1.717	0.144
	S × NP	5	1.366	0.249		0.419	0.834
Seed	S	1	34.57	<0.05	Allocation to leaf	0.675	0.414
number	NP	5	17.348	<0.05		7.14	<0.05
	S × NP	5	1.435	0.224		2.365	0.05
Root mass	S	1	11.99	<0.05	Allocation to	6.013	<0.05
	NP	5	13.663	<0.05	reproduction	7.12	<0.05
	S × NP	5	1.263	0.291		0.663	0.653
Stem	S	1	7.072	<0.05	Germination	3.44	<0.05
mass	NP	5	18.638	<0.05	percentage	12.111	<0.05
	S × NP	5	0.323	0.897		8.106	<0.05

Note: S, germination seasons; NP, including nitrogen and precipitation plus nitrogen treatments (CK, N1, N2, N3, W1N1 and W2N1). Control treatment, CK; 30 kg N ha^{-1} yr^{-1}, N1; 60 kg N ha^{-1} yr^{-1}, N2; 120 kg N ha^{-1} yr^{-1}, N3; +30% increases in precipitation plus 30 kg N ha^{-1} yr^{-1}, W1N1; +50% increases in precipitation plus 30 kg N ha^{-1} yr^{-1}, W2N1.

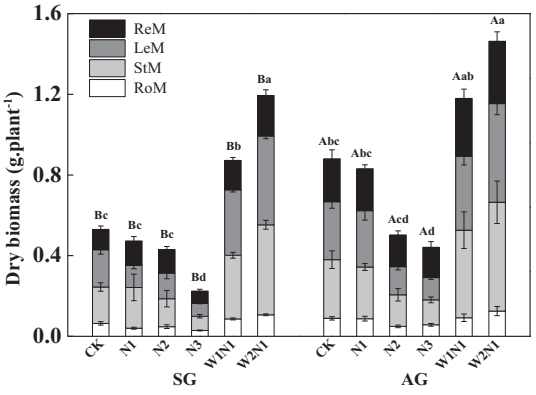

Fig. 3. Effects of increased nitrogen and precipitation plus nitrogen treatments on dry mass accumulation of spring- and autumn-germinated plants of *Erodium oxyrhynchum*. Note: Spring-germinated plants, SG; autumn-germinated plants, AG; control treatment, CK; 30 kg N ha^{-1} yr^{-1}, N1; 60 kg N ha^{-1} yr^{-1}, N2; 120 kg N ha^{-1} yr^{-1}, N3; + 30% increases in precipitation plus 30 kg N ha^{-1} yr^{-1}, W1N1; +50% increases in precipitation plus 30 kg N ha^{-1} yr^{-1}, W2N1. ReM, reproduction mass; LeM, leaf mass; StM, stem mass; RoM, root mass. Values represent means ± SE. Significant difference was observed among all treatments, different lowercase letters indicate significant differences among increased nitrogen and precipitation plus nitrogen treatments (CK, N1, N2, N3, W1N1 and W2N1) for SG and AG (Tukey HSD test, N = 8, $p < 0.05$), and different uppercase letters indicate significant differences between SG and AG at the same increased nitrogen or precipitation plus nitrogen treatments (t-test, N = 4, $p < 0.05$).

increased biomass accumulation of SG and AG plants significantly ($p < 0.05$, Table 2). With increased nitrogen (N1, N2, N3), SG and AG plants allocated more biomass into roots and reproduction and allocated less biomass into leaves (Fig. 4), but stem allocation of SG and AG plants showed almost no change. With precipitation plus nitrogen treatments, SG and AG plants allocated less biomass into roots and allocated significantly more biomass into stems; however, almost no significant effects on leaf and reproductive allocation were observed.

3.5. Offspring (seeds) germination

In the control (CK), germination percentage of offspring (seeds) produced by SG plants was 33.0%, while germination percentage of offspring (seeds) produced by AG plants was only 2.0% ($p < 0.05$, Table 2

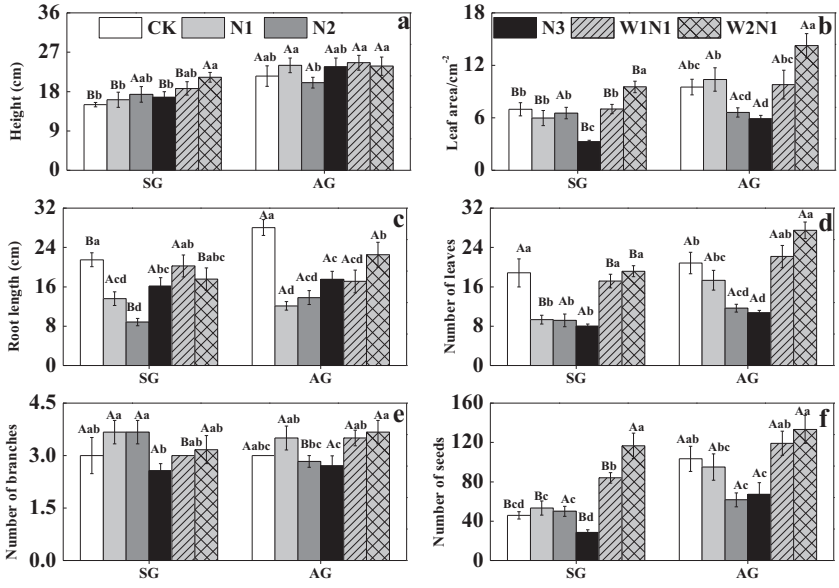

Fig. 2. Effects of increased nitrogen and precipitation plus nitrogen treatments on plant traits of spring- and autumn-germinated plants of *Erodium oxyrhynchum*. Note: Spring-germinated plants, SG; autumn-germinated plants, AG; control treatment, CK; 30 kg N ha^{-1} yr^{-1}, N1; 60 kg N ha^{-1} yr^{-1}, N2; 120 kg N ha^{-1} yr^{-1}, N3; +30% increases in precipitation plus 30 kg N ha^{-1} yr^{-1}, W1N1; +50% increases in precipitation plus 30 kg N ha^{-1} yr^{-1}, W2N1. Values represent means ± SE. Significant difference was observed among all treatments, different lowercase letters indicate significant differences among increased nitrogen and precipitation plus nitrogen treatments (CK, N1, N2, N3, W1N1 and W2N1) for SG and AG (Tukey HSD test, N = 8, $p < 0.05$), and different uppercase letters indicate significant differences between SG and AG at the same increased nitrogen or precipitation plus nitrogen treatments (t-test, N = 4, $p < 0.05$).

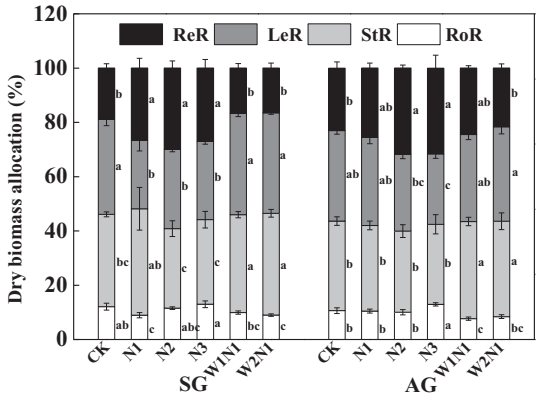

Fig. 4. Effects of increased nitrogen and precipitation plus nitrogen treatments on biomass allocation of spring- and autumn-germinated plants of *Erodium oxyrhynchum*. Note: Spring-germinated plants, SG; autumn-germinated plants, AG; control treatment, CK; 30 kg N ha^{-1} yr^{-1}, N1; 60 kg N ha^{-1} yr^{-1}, N2; 120 kg N ha^{-1} yr^{-1}, N3; +30% increases in precipitation plus 60 kg N ha^{-1} yr^{-1}, W1N1; +50% increases in precipitation plus 60 kg N ha^{-1} yr^{-1}, W2N1. ReP = reproductive mass / total mass × 100%; RoP = roots mass / total mass × 100%; StP = stems mass / total mass × 100%; LeP = leaves mass / total mass × 100%. Values represent means ± SE. Significant difference was observed among all treatments, different lowercase letters indicate significant differences among increased nitrogen and precipitation plus nitrogen treatments (CK, N1, N2, N3, W1N1 and W2N1) for SG and AG (Tukey HSD test, N = 8, $p < 0.05$).

and Fig. 5). With increased nitrogen (N1, N2, N3), germination percentage of offspring (seeds) produced by SG and AG plants first increased and then decreased. Precipitation plus nitrogen treatments (W1N1 and W2N1) decreased germination percentage of offspring produced by SG plants, from 33.0% (CK) to 16.0% (W1N1) and 17.0% (W2N1), whereas for offspring produced by AG plants, germination percentage increased from 2.0% (CK) to 45.0% (W1N1) and 9.0% (W2N1) (Fig. 5).

4. Discussion

A changing global environment will especially affect the growth of plants in arid and semiarid regions (Xu et al., 2016).We took spring- and autumn-germinating ephemeral plants of *E. oxyrhynchum* as the object of research for the first time to determine the effects of increased nitrogen and precipitation plus nitrogen on the life history of plants from different seasons, in an attempt to understand the responses of winter annual and spring ephemeral plants to global change.

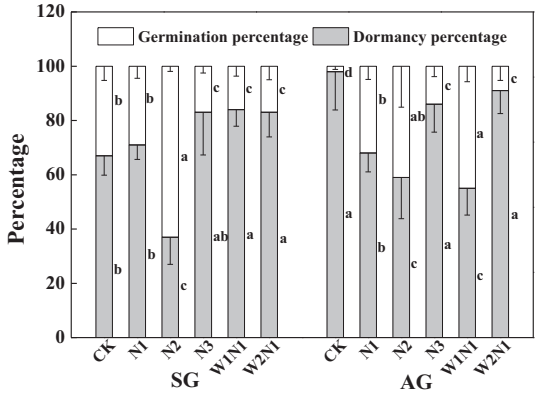

Fig. 5. Effects of increased nitrogen and precipitation plus nitrogen treatments on offspring (seed) germination from spring- and autumn-germinated plants of *Erodium oxyrhynchum* incubated in light/dark at 25/10 °C. Note: Spring-germinated plants, SG; autumn-germinated plants, AG; control treatment, CK; 30 kg N ha^{-1} yr^{-1}, N1; 60 kg N ha^{-1} yr^{-1}, N2; 120 kg N ha^{-1} yr^{-1}, N3; +30% increases in precipitation plus 60 kg N ha^{-1} yr^{-1}, W1N1; +50% increases in precipitation plus 60 kg N ha^{-1} yr^{-1}, W2N1. Values represent means ± SE. Significant difference was observed among all treatments, different lowercase letters indicate significant differences among increased nitrogen and precipitation plus nitrogen treatments (CK, N1, N2, N3, W1N1 and W2N1) for SG and AG (Tukey HSD test, N = 8, $p < 0.05$).

In the control, the survival of AG plants was significantly lower than that of SG plants, supporting the hypothesis. This result was mainly because AG plants experience a low temperature and arid environment up to four months in winter (Supplementary Fig. 2, Chen et al., 2019, unpublished), and severe damage to roots, stems and leaves leads to seedling deaths (Fan et al., 2014). Increased nitrogen and precipitation plus nitrogen treatments improved the survival of SG and AG plants significantly (Fig. 1a–b), which refuted the hypothesis. Nitrogen and precipitation are essential for plant growth, especially in the seedling stage, increased precipitation and nitrogen improve the barren and arid desert environment, which promotes seedling establishment (Donovan and Richards, 2000; Invers et al., 2004). Phenology is well recognized as one of the most sensitive indicators of environmental change (Han et al., 2015). In our study, increased nitrogen had almost no significant impact on the phenophase of SG and AG plants, but precipitation plus nitrogen treatments delayed the reproductive stage and extended the life cycle of SG and AG plants significantly, thereby partially supporting our hypothesis. When the reproduction stage is delayed, plants spend more time on vegetative growth, thereby ensuring plants produce more seeds during the reproduction stage (Lechowicz and Blais, 2010). This conclusion is consistent with the findings for *Potentilla tanacetifolia* of the importance of the maternal environment effect on seed production (Li et al., 2011). Therefore, future increased nitrogen deposition and precipitation will improve seedlings establishment and plant growth under a winter annual and spring ephemeral species in an arid and semi-arid ecosystems.

A positive correlation between plant traits and biomass accumulation has been confirmed in most herb species (Augspurger et al., 1985; Lu et al., 2014). In our study, increased nitrogen decreased most plant traits (leaf area, root length, leaf number, branch number and seed number) of SG and AG plants and had almost no effect on the height of SG and AG plants. Thus, biomass accumulation of SG and AG plants showed a decreasing trend with increased nitrogen (Fig. 3). However, Zhou et al. (2014) found that the biomass accumulation of *E. oxyrhynchum* increased significantly with increased nitrogen in 2011, which is the exact opposite of our results. We speculate the significant difference in biomass accumulation maybe caused by a different precipitation pattern between 2011 and 2017. In 2017, almost no events of >10 cm of precipitation occurred in the study area (Supplementary Fig. 2, Chen et al., 2018, unpublished), but in 2011, events with >10 cm of precipitation occurred 4 times, and the total amount of precipitation in 2017 was less than half that in 2011 (Zhou et al., 2015). Thus, soil moisture shortage limited the improvement of nitrogen on plant growth and intensified stress from soil acidification by excessive nitrogen. Many studies also show that increased nitrogen inhibits photosynthesis and decreases herbaceous plant biomass under low soil moisture conditions, especially in grassland ecosystems (Yahdjian and Sala, 2010; Yang et al., 2011). Similarly, in the Gurbantunggut Desert, experiments with increasing snow and nitrogen also showed that nitrogen addition promoted the growth of ephemeral plants under increased snow, but nitrogen addition limited the growth of ephemeral plants under decreased snow (Fan et al., 2013).Perhaps, sufficient moisture is an important prerequisite for nitrogen to promote plant growth. In addition, Zhou et al. (2015) did not distinguish between spring-and autumn-germinated plants of *E. oxyrhynchum*, which also limits the comparability of results. In our study, precipitation plus nitrogen treatments also significantly promoted plant growth and biomass accumulation of SG and AG plants, which confirmed the effects of precipitation on nitrogen utilization by the plants. Thus, our findings may correct previous conclusions on nitrogen promotion of ephemeral plant growth in the Gurbantunggut Desert. In addition, the similarity in responses of SG and AG plants to nitrogen and precipitation in most life history traits indicated that plants of the same species have consistent mechanisms

for use of resources, but the response may also be different due to the difference in plant size and growing period. Therefore, future increases in nitrogen deposition and precipitation will also affect the growth of SG and AG plants, but the response of SG plants to global change will be more sensitive than that of AG plants.

Biomass allocation is a key process of plant growth (Sugiura et al., 2016). Our research indicated that root, stem, leaf and reproduction allocation of AG plants was similar to that of SG plants in the control and precipitation plus nitrogen treatments, which is a result consistent with the results for four ephemeral *Trigonella* species (Yao and Tan, 2005). Therefore, plants could adjust the biomass allocation to various organs to keep relatively stable under suitable conditions. With increased nitrogen, SG and AG plants allocated more biomass to reproductive organs, which may be because when nitrogen exceeds the tolerable range for plant growth under low precipitation, nitrogen will turn into a stress factor that inhibits plant growth. At this time, plants allocate more biomass into roots in order to absorb more nutrients (Casper et al., 1998; Defrenet et al., 2016) and allocate more biomass into reproductive organs in order to produce more seeds (Throop, 2005; Burns et al., 2017). Therefore, change in biomass allocation is an important strategy for plants to maintain the continuation of populations in a changing environment.

The seed stage is the most tolerant to environmental stress during the life cycle of plants, and dormancy is conducive to the seed entering the seedling stage under conditions suitable for seed germination (Qu and Huang, 2005). In the case of high reproduction output, plants increase the dormancy percentage of seeds to avoid overcrowding in the following year (Holzapfel et al., 2006; Tielborger and Petru, 2010). Our results showed that seeds with nondormancy (ND) produced by SG and AG plants significantly increased with increased nitrogen (Fig. 5). The result indicated that seeds with ND could germinate quickly in a suitable environment, which is conducive to occupying living space in the community. Under precipitation plus nitrogen treatments, seeds that remained in physical dormancy (PY) produced by SG plants increased with high reproductive output, which is consistent with the conclusion of high reproduction and avoidance of overcrowding in the following year. However, AG plants produced more seeds with ND under precipitation plus nitrogen treatments, which may be related to spreading the germination risk in time in order to avoid the risk of population extinction from a single germination. Perhaps, this offspring dormancy strategy of SG and AG plants is in response to the changing environment of the Gurbantunggut Desert, and such a strategy avoids not only the risk of population extinction in a harsh environment but also reduces intraspecific competition in a suitable years. Therefore, the offspring seed dormancy strategy of SG and AG plants is likely to be an important reason for determining that *E. oxyrhynchum* has become the dominant species of the ephemeral plant community in the Gurbantunggut Desert.

In conclusion, for both AG and SG plants, precipitation plus nitrogen treatments prolonged the life cycle and increased biomass accumulation and seed production, but increased nitrogen decreased plant growth and biomass accumulation and increased the proportion of biomass allocated to reproduction and roots while decreasing the allocation to leaf. None of these results supported our hypothesis that AG and SG plants would respond differently to additional nitrogen and precipitation. In the context of nitrogen deposition and precipitation changing, increases in biomass and seed production of SG and AG plants increase the competitive advantage of *E. oxyrhynchum* populations in the community. For offspring dormancy, SG and AG plants produced more nondormancy seeds with increased nitrogen but produced more seeds of PY under precipitation plus nitrogen treatments. Thus, these results refuted our hypothesis. SG and AG plants produced more nondormancy seeds in a harsh environment in order to occupy habitat rapidly in the next year or produced more dormancy seeds in a suitable years intended for avoiding interspecific competition. Finally, the ability of some seeds to germinate in autumn and others in spring will be maintained because of the similar responses of SG and AG plants to increased nitrogen deposition and precipitation in most life history traits.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.12.368.

Acknowledgments

Sources of Funds for this study were provided by the National Natural Science Foundation of China (31660162, 31570529) and Youth Innovation Promotion Association of Chinese Academy of Sciences (2018477). We are grateful to our associate editor Professor Elena PAOLETTI and the anonymous reviewers for their thoughtful comments that substantially improved the manuscript.

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